

PROECHIMYS SEMISPINOSUS (RODENTIA:
ECHIMYIDAE): DISTRIBUTION, TYPE
LOCALITY, AND TAXONOMIC HISTORY

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Abstract.—The type locality of *Proechimys semispinosus* (Tomes) has been alleged to be Gualaquiza, in the lowland forests of southeastern Ecuador. A review of the travels of the collector Louis Fraser, and examination of the content of reports based on the mammals he collected, plus the comparison of the type specimen with samples representing several species of *Proechimys* from Central and South America, indicate that the type did not come from Gualaquiza. The type locality of *P. semispinosus* is corrected to Esmeraldas, on the Pacific coast of Ecuador.

The specimens on which Tomes (1860b) based the name *Echimys semispinosus* were collected by Louis Fraser in Ecuador and alleged (Allen 1916) to have come from Gualaquiza, a community on the Rio Santiago in the Province of Morona-Santiago. This site (03°24'S, 78°33'W *vide* Paynter and Traylor 1977) is east of the Andes, at 750 meters elevation, in the tropical zone of the western Amazonian forests. I have concluded, however, from my examination of the skull of the type (British Museum [Nat. Hist.] 7.1.1.173), that it is unlike skulls of any of the species of *Proechimys* known to me from South America east of the Andes. Instead, it has the cranial features that characterize populations of *Proechimys* found west of the Andes along the Pacific lowlands of Colombia and Ecuador and northward through Central America to Honduras that currently are known in the literature as either *Proechimys centralis* or *P. semispinosus*.

The present report is the result of my examination of specimens and search of the literature in an attempt to determine the provenance of the specimens that Tomes used in describing *P. semispinosus*. In addition to the examination and comparison of specimens, including types, I have explored three main sources of information: the published history of the use of the name *P. semispinosus*, accounts of Fraser's travels in Ecuador, and the content of reports on the mammals Fraser collected.

Taxonomic History

1860

Tomes described *Echimys semispinosus* based primarily on one of "three specimens . . . received in spirits, all of which were females; one of them contained two young" (1860b:267–268), and figured the skull of one of these. The specimens had been collected by Fraser at an unspecified locality in Ecuador. Tomes introduced this account by stating (p. 265), "In my first notes [Tomes 1859] on Mammals, collected by Mr. Fraser, I included the *Echimys cayennensis* from the examination of a specimen which had lost the tail, and was otherwise in an unsatisfactory condition. Other and better specimens of *Echimys* having been

received, I have been able to make out clearly that they represent a new and well-marked species, and that the former specimen was similar to them."

1889

True recorded *Echinomys semispinosus* from Nicaragua and Costa Rica.

1896

Thomas described *Echinomys centralis* (type locality: San Emilio, south end of Lake Nicaragua) and said that True's (1889) report was based on the same species. Thomas also stated (p. 312), "Both in the Merida and Bogota collections there occur specimens of the genus *Echinomys* which, on account of their (in comparison with other species) 'very dark brown colour' and other characters, may fairly be assigned to *E. semispinosus*, Tomes, especially if, as seems to be the case, Tomes's woodcut of the skull is incorrect in details." Thus Thomas assigned seven specimens (p. 313) from Colombia to *E. semispinosus*.

1897

Thomas, in his description of *Echimys gymnurus* (= *Hoplomys gymnurus*), remarked (p. 551), "This handsome *Echimys* differs from Tomes's *E. semispinosus*, also from Ecuador, but without exact locality, by its richer rufous colour In all these points the Bogota *Echimys* assigned last year to *E. semispinosus* agrees much better with Tomes's description than does that [*E. gymnurus*] brought home by Mr. Rosenberg, in spite of the Ecuadoran locality of the latter."

1898

Thomas recanted his assignment of the Bogota specimens (which he here named *Echimys chrysaеolus*) to *E. semispinosus* Tomes, and decided that *E. semispinosus* was allied with the Nicaraguan specimens he had already described (1896) as *E. centralis*. This resulted from the discovery of "a dark brown *Echimys* marked, in what appears to be a hand writing similar to that on some of Fraser's labels, '*Echimys semispinosus*,'" among specimens that had been overlooked for many years in rooms of the Zoological Society. Thomas stated (p. 244), "This [specimen] so precisely agrees with Tomes's description of that animal, that there can be no reasonable doubt that it is one of the original specimens collected by Fraser and referred to in Tomes's paper." The label may have lacked notation of locality for Thomas failed to mention one.

1899

Allen proposed the name *Proechimys* (type-species, *Echimys trinitatus* Allen and Chapman) to include, among others, the species *P. semispinosus*.

1900

Thomas described *Proechimys rosa* (type locality, Santa Rosa, Prov. El Oro, Ecuador), *P. centralis panamensis* (type locality, "Savanna near Panama") and *P. centralis chiriquinus* (type locality, Bugava [= Bugaba], Prov. Chiriquí, Panama). Thomas allied *P. semispinosus* with *P. decumanus* (described by Thomas 1899, from Chongon, Prov. Guayas, Ecuador), but said that *P. rosa* was allied to the Central American species *P. centralis*.

1901

Bangs described *Proechimys burrus* (type locality, Isla San Miguel, Golfo de Panamá), which he allied with *P. centralis*.

1905

Bangs described *Proechimys gorgonae* (type locality, Isla Gorgona Colombia), which he allied with *P. centralis panamensis*.

1911

Thomas described *P. semispinosus calidior* (type locality, San Javier, Prov. Esmeraldas, Ecuador), calling it "A rufous lowland representative of true *semispinosus*." In a footnote (p. 254), he said that the type of *P. semispinosus* was British Museum (NH) number 7.1.1.173, which means that the specimen was the 173rd cataloged on 1 January 1907.

1914

Hollister described *Proechimys rubellus* from Costa Rica. He said the type came from the Angostura Valley, but as True (1889:467) had stated earlier and as indicated on the label of the holotype, the actual collection site is Pacuare.

1914

Thomas described *P. centralis colombianus* (type locality, Condoto, Depto. Chocó, Colombia) and compared it to "*Proechimys xanthaeolus*," apparently a lapsus for *P. chrysaеolus*.

1916

Allen wrote (pp. 206–207), "The type locality of *Echimys semispinosus* Tómes, according to Thomas (on the back of label), is Gualaquiza, Ecuador, this being the specimen from which the skull was figured. Three specimens of this species were received 'in spirits, all of which were females; one of them contained two young' (Tomes, P. Z. S., 1860, p. 267). Two of these specimens are now in the British Museum, 'evidently skinned out of spirit and much discolored,' as stated on the labels. I omitted to examine the type skull figured by Tómes, but from an examination of Tómes's figure it is too adult to have belonged to either of these two skins, which are only about half grown. The skin of the third specimen, doubtless the adult female mentioned by Tómes, and the one to which the figured skull belonged, has apparently been lost."

1920

Goldman arranged all of the named forms of Central American *Proechimys* as subspecies of *P. semispinosus*, except for *P. centralis chiriquinus*, which he treated as a synonym of *P. semispinosus panamensis*.

1935

Tate in his review of the taxonomy of *Proechimys*, listed *P. semispinosus* with western Amazonian species on the basis of the alleged type locality.

1937

Bole described *P. semispinosus goldmani* from Altos Cacao, Prov. Veraguas, Panama.

1940

Ellerman listed all named forms of *Proechimys semispinosus* as subspecies or synonyms of *P. cayennensis* (Desmarest), but remarked that if this be incorrect, *burrus*, *centralis*, *panamensis* (with *chiriquinus* a synonym), *rubellus*, *colombianus*, and *calidior* should be considered races of *P. semispinosus*.

1944

Osgood said that the type of *Proechimys semispinosus* was a skull only and that, as the type locality was in southeastern Ecuador, populations from northern Peru (Huallaga River) probably were identical or closely related. He also assigned a series of specimens from Lagunas in east central Peru to *P. semispinosus*. Osgood believed *P. semispinosus calidior* to be a "slight subspecies of *semispinosus*" allied with *P. rosa* and Central American forms.

1946

Kellogg described *P. semispinosus ignotus* from Isla San José, Golfo de Panamá, Panama.

1946

Goodwin treated Costa Rican *centralis*, *panamensis*, and *rubellus* as subspecies of *P. cayennensis*.

1948

HersHKovitz considered *P. semispinosus* a subspecies of *P. guyannensis* (E. Geoffroy), the senior synonym of *P. cayennensis* (Desmarest). He described (p. 138) *P. quadruplicatus* from Isla Llunchi, Río Napo, Ecuador, and referred to it the specimens from Lagunas, Peru, that Osgood (1944) had assumed to be representative of *P. semispinosus*. Based on the enamel patterns of the cheekteeth, he said that two kinds of *Proechimys* occur in Central America; those assignable to *P. guyannensis* as subspecies, and others (including *ignotus*, which he elevated to species rank) referable to the *P. quadruplicatus* group.

1948

Moojen treated *P. semispinosus* as a species to which he assigned all of the named forms of *Proechimys* from Central America and western Colombia and Ecuador as well as the Amazon basin populations he believed were represented by the names *gularis*, *hilda*, *kermitti*, *liminalis*, and *amphichoricus*. Moojen described the last two taxa as new subspecies.

1959

Hall and Kelson followed Moojen (1948) and recognized *burrus*, *centralis*, *goldmani*, *ignotus*, *panamensis* (*chiriquinus* a synonym), and *rubellus* as subspecies of *P. semispinosus*.

1961

Cabrera followed Moojen's (1948) application of *P. semispinosus* to the assignment of names to South American *Proechimys*, with the following exceptions: *colombianus*, *decumanus*, and *gorgonae* treated as subspecies of *P. guyannensis*; *gularis* (*sensu* Moojen 1948; not of Thomas 1911) assigned to *P. quadruplicatus* HersHKovitz.

1966

Handley considered the taxa *burrus*, *goldmani*, *ignotus*, and *panamensis* to be subspecies of Panamanian *P. semispinosus*.

1972

Patton and Gardner used the name *P. semispinosus* for Costa Rican topotypes of *P. rubellus*.

1976

Handley identified some Venezuelan populations as *P. semispinosus*.

1976

Reig and Useche used *P. centralis* for the Costa Rican *Proechimys* that Patton and Gardner (1972) had called *P. semispinosus*, stating that they preferred to follow Thomas's original application of *P. centralis* to all Central American members of the genus.

1981

Hall applied *P. semispinosus* in the same way the name was used by Hall and Kelson (1959).

Fraser's Travels in Ecuador

I have gleaned information on Louis Fraser's travels in Ecuador, from the time he arrived in Guayaquil, 20 September 1857, until he left Esmeraldas at the end of December 1859, from three reports by Tomes (1859, 1860a, b) on the mammals, several reports on the birds by Sclater (1859a, b, c, 1860a, b, c, d, e), and published extracts of letters written from Ecuador by Fraser (1858a, b, 1859a, b, c, d, 1860).

After a brief stay in Guayaquil, Fraser proceeded to Cuenca, arriving on 6 October 1857 and remaining there through November. Then he journeyed to Gualaquiza where he worked from December 1857 through February 1858, except for a two-week period in Zamora during January.

Fraser left Gualaquiza for Cuenca on 1 March (arriving 5 March) where he collected through April and May before proceeding to Riobamba. He worked in or near Riobamba during June and again in August on his return from Quito before continuing on to Pallatanga. His collections in the Pallatanga area, with trips to Chillanes, were made from the latter part of August through December 1858.

Leaving Pallatanga in mid-January 1859, Fraser collected on the slopes of Chimborazo north of Riobamba in February on his way to Quito. March, April, May, and part of June were spent in the vicinity of Quito and on the slopes of Pichincha as well as on the western slopes of the Andes northwest of Quito.

Fraser traveled southward from Quito to Babahoya where he stayed from 10 July through part of September. Then he went on to Guayaquil where, in the beginning of October, he left by ship for Esmeraldas. Fraser remained in Esmeraldas until the end of December and then left Ecuador for Guatemala.

Tomes' Reports on Fraser's Ecuadoran Mammals

Like many naturalist travellers of his day, Fraser collected a variety of vertebrates, invertebrates, and plants, but concentrated on birds. Among the several reports based wholly or in part on the mammals he collected in Ecuador are three major ones by Tomes published in the Proceedings of the Zoological Society of London (1859, 1860a, b).

In the first report, "Notes on a Collection of Mammalia made by Mr. Fraser at Gualaquiza," Tomes (1859) listed 17 taxa (some unidentified). Among these was (p. 548) "*Echimys cayenensis*, Geoff. A thickly-spined and rather large ex-

ample, apparently somewhat more strongly tinged with rufous than the illustration given by Mr. Waterhouse, or than either of those given by M. Pictet." The list was incomplete, however, for Fraser (1858b:6158) said in a letter dated Gualaquiza, 13 February 1858, that he had "skulls of tapir and white-lipped peccary," which are missing from Tomes' list. Moreover, not all of the animals that Tomes listed actually came from Gualaquiza. Fraser (1858a:5942) stated in a letter from Cuenca dated 21 October 1857 that he had "three or four Mammalia" on hand before he went into the southeastern lowlands of Ecuador. While at Gualaquiza, Fraser took a side trip to Zamora and collected mammals there. Nevertheless, there is no reason to question Gualaquiza as the place of origin of the rat Tomes (1859:548) reported as "*Echimys cayenensis*."

The next report (Tomes 1860a), "Notes on a Second Collection of Mammalia made by Mr. Fraser in the Republic of Ecuador," listed 15 identified and unidentified species, two of which (*Hesperomys latimanus* and *H. minutus*) were described as new. At the end of the report, Tomes described two species (*Hesperomys bicolor* and *H. aureus*) based on specimens previously listed in his first report (Tomes 1859). With the exception of these two last named species and the *Diphylla ecaudata* (which came from "Rio Napo" and had been given to Fraser), the mammals of the second report were believed by Tomes (1860:211), "to have been collected at Pallatanga on the western slope of the Cordillera: but the exact locality is not certain, from the specimens having been unfortunately mixed together." Tomes gave evidence that Pallatanga was the origin of some of this material. Some specimens, however, may have come from Chillanes (known to have been visited by Fraser during his stay at Pallatanga), or from the vicinity of Riobamba where Fraser worked before going to Pallatanga (but there is no record that he collected mammals there).

The final report (Tomes 1860b), "Notes on a Third Collection of Mammalia made by Mr. Fraser in the Republic of Ecuador," contained 21 taxa, of which *Hesperomys caliginosus*, *H. albigularis*, and *Echimys semispinosus* were described as new. Pallatanga was indicated as the source of *H. albigularis*, but no locality data were given for the other two newly described species. Actually, localities were mentioned for only nine of the 21 taxa that Tomes listed. However, attention to dates, information from letters, and subsequent designations of type localities result in coastal Ecuador indicated for 1; Cuenca for 2; Gualaquiza, 3; Zamora, 2; Pallatanga, 2; Esmeraldas, 5; and unknown, 6. Of the three taxa from Gualaquiza, two are represented by the tapir and white-lipped peccary skulls first mentioned in Fraser's (1858b:6158) letter from Gualaquiza. The third is *Echimys semispinosus* represented by three specimens including the type, which Allen (1916) said, based on Thomas' determination, came from Gualaquiza.

Discussion

Fraser collected four specimens of *Proechimys*: the specimen from Gualaquiza first reported by Tomes in 1859 as *Echimys cayenensis* and three females in spirits reported without locality by Tomes in 1860. One of these three, an adult with two embryos, was the subject of the illustrations and measurements given by Tomes (1860b) in his description of *Echimys semispinosus* and to which he said the Gualaquiza specimen was "similar." It is apparently this specimen that was

later given British Museum (NH) catalog number 7.1.1.173, and is now labelled as the type of *Echimys semispinosus* Tomes.

The skin of the holotype now lacks a tail. The tail was present when Tomes (1860b) described *P. semispinosus* because he said it measured 5 inches, 6 lines (= 139.7 mm). The skull of the holotype is in good condition. These clues confirm that the skin and skull presently labelled as the holotype of *P. semispinosus* do not represent the animal Tomes reported in 1859 from Gualaquiza, because Tomes (1860b) commented on the unsatisfactory condition of that specimen and noted that it lacked a tail.

It can be inferred from Thomas' (1896, 1897) writings that the holotype of *P. semispinosus* had been lost for some time before it was located among some specimens in rooms of the Zoological Society of London (Thomas 1898). Prior to its discovery, Thomas had assumed that material he later named *P. chrysaëolus* (Thomas, 1898) was representative of *P. semispinosus*. His confidence in that assumption was sufficiently strong for him to suggest that certain details in Tomes' figure of the skull were incorrect (Thomas 1896:312). I presume that the details Thomas was referring to included the strongly-developed parietal ridges. A single, strongly-developed ridge across the parietals is a feature characteristic of all populations of *Proechimys* found in Central America and in northern South America west of the Andes, with the exception of *P. decumanus*. Elsewhere in South America, parietal ridges, if present, are usually discontinuous, with the posterior component dorsal to and overlapping the anterior component. Specimens having a single ridge across each parietal are rare in Amazonian South America and such ridges are weakly developed, often inconspicuous.

The label on the skin of the type has the following information: *Proechimys semispinosus* Tomes; BM 7.1.1.173; Tomes collection; collector L. Fraser 1; Gualaquiza; hindfoot 46, ear 21; P. Z. S. London, 1858, p. 548 and 1860, p. 265. The catalog number indicates that this specimen was catalogued on 1 January 1907, the same date that other specimens Tomes described were catalogued (e.g., *Marmosa waterhousei*, BN 7.1.1.215; *Oryzomys albigularis*, BM 7.1.1.105; *O. caliginosus*, BM 7.1.1.128; *Thomasomys aureus*, BM 7.1.1.104). Not all of Fraser's material reported on by Tomes was catalogued on that date because the types of *Oryzomys phaeopus* Thomas, 1894 (BM 59.11.1.9), and *O. dryas* Thomas, 1898 (BM 59.11.1.11), from the same collection had been catalogued in 1859. This information suggests that the types of all of the species described by Tomes from Fraser's Ecuadoran collections were among those specimens found at the Zoological Society of London.

The label information that the skin is Fraser's number 1 is difficult to interpret. The specimen is neither the first that Fraser collected in Ecuador nor the first mammal because he said he had "three or four Mammalia" (Fraser 1858a:5942) from Cuenca where he began collecting and where *Proechimys* does not occur. One could argue that Fraser's number 1 is correct, that he used a separate series for each year, and that the holotype of *P. semispinosus* was the first prepared in 1858 and, therefore, definitely came from Gualaquiza. However, judging by Fraser's numbers for birds cited in some of Sclater's reports (1859c, 1860a, d, e) it appears that Fraser used a single series of field numbers during 1858 and 1859 and presumably from the time he began collecting in 1857. Probably all of his specimens or at least all of the vertebrates were included in the single series of

numbers. Fraser's number 1705 (the holotype of *Oryzomys albigularis*) is close to Fraser's numbers that Sclater (1860a) cited for birds, also from Pallatanga. Therefore, the indication that the type of *P. semispinosus* was Fraser's first Ecuadoran mammal specimen must be incorrect.

The only *Proechimys* whose features resemble those of the type of *P. semispinosus* and may be expected to occur in the vicinity of Gualaquiza is *P. quadruplicatus* Hershkovitz, 1948. Although some features of *P. quadruplicatus* are similar to those of the type as well as to specimens identified as *P. semispinosus* by Patton and Gardner (1972) from Central America and the Pacific lowlands of Colombia and Ecuador, the skulls are clearly different. Contrasted with *P. quadruplicatus*, the skull of the type of *P. semispinosus* has a broader braincase, well-developed continuous ridges across the parietals, more posterior termination of the nasals in relation to the fronto-maxillary suture, and a less complex pattern of enamel folds on the cheek teeth ($\frac{3-3-3-4}{4-3-3-3}$ versus $\frac{4-4-4-4}{4-3-3-3}$ in *P. quadruplicatus*).

So where could Fraser have collected the type of *P. semispinosus*? *Proechimys* occurs in only four of the localities where Fraser collected: Gualaquiza, Babahoya, Guayaquil, and Esmeraldas. One of the first places where Fraser worked was Gualaquiza where he took the specimen Tomes (1859) reported as "*Echimys cayenensis*." Tomes' (1860b) third account listed taxa from several places in Ecuador, including Gualaquiza. However, the only Gualaquizan mammals of this account were larger species; all of the small mammals Fraser collected at Gualaquiza had been covered in Tomes' first report (1859). There is no evidence that Fraser collected mammals in Babahoya or Guayaquil. Esmeraldas was the last Ecuadoran locality visited by Fraser and, in my opinion, is the most likely origin of the three specimens on which Tomes based his description of *P. semispinosus*. Furthermore, a species of *Proechimys* characterized by all of the features demonstrated by the type of *P. semispinosus* is common in the vicinity of Esmeraldas. Coincidentally, Esmeraldas was designated by Allen (1913:537) as the type locality of *Oryzomys caliginosus*, the other species Tomes (1860b) described without locality in his third report.

Conclusions

A review of Fraser's travels in Ecuador, an examination of the content of Tomes' (1859, 1860a, b) main reports on the mammals Fraser collected, and the direct comparison of the type specimen with samples of several species of *Proechimys* from Central and South America indicate that Gualaquiza is not the source of the type of *P. semispinosus*. The type locality is here corrected to Esmeraldas, Prov. Esmeraldas, on the Pacific coast of Ecuador.

Much of the confusion regarding the correct allocation of the name *P. semispinosus* resulted from the following factors: 1) The presumed loss of the type and Thomas' faith that material from "near Bogota" was representative of true *semispinosus*; 2) the belief (subsequent to the rediscovery of the type) that the type locality was Gualaquiza and, therefore, the zoogeographically-based conclusion that the name was applicable to populations east of the Andes; and 3) the obvious similarity between the type specimen and characteristics seen in populations of *Proechimys* found in Central America and the Pacific lowlands of Colombia and Ecuador.

Because of the correction of the type locality, *P. semispinosus calidior* becomes a subjective junior synonym of *P. semispinosus*. The epithets *burrus*, *centralis*, *chiriquinus*, *colombianus*, *goldmani*, *gorgonae*, *ignotus*, *panamensis*, *rosa*, and *rubellus* are available as names for populations of *P. semispinosus*. Of these, *centralis* applies to the populations in Nicaragua, Honduras, and northern Costa Rica. The southernmost population of Ecuador should be known as *P. semispinosus rosa*. Allocation of most of the remaining names awaits a taxonomic revision of the species.

Hershkovitz (1948) allied *P. ignotus* with his *P. quadruplicatus* group; however, several populations of *P. semispinosus* are superficially similar in dental structure to *P. quadruplicatus* and *ignotus* is best treated as a subspecies of *P. semispinosus*.

The Central American distribution of *P. semispinosus* extends from southeastern Honduras and eastern Nicaragua through Costa Rica and Panama including the Islas las Perlas (see Hall 1981:873). In South America, the range is west of the Andes from the Choco of Colombia (including Isla Gorgona) to southwestern Ecuador. A record for extreme northwestern Peru (Tumbez, Rio Tumbez; see Thomas 1882:101) has not been confirmed. Those specimens may represent *P. decumanus* Thomas, 1899, which occurs in that region and is sympatric with *P. semispinosus rosa* in southwestern Ecuador (provinces of Guayas and El Oro).

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